The Royal Society

State-dependent shifts between nocturnal and diurnal activity in salmon

Neil B. Metcalfe*, **Neil H. C. Fraser and Martin D. Burns**

Fish Biology Group, Graham Kerr Building, Institute of Biomedical & Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK

Animal species have usually evolved to be active at a specific time of the daily cycle, and so are either diurnal, nocturnal or crepuscular. However, we show here that the daily timing of activity in juvenile Atlantic salmon is related to the life-history strategy that they have adopted (i.e. the age at which they will migrate to the sea) and their current state (body size/relative nutritional state). Salmon can detect food more easily by day than by night, but the risk of predation is greater. Nocturnal foraging should generally be preferred, but the greater the need for growth, the greater should be the shift towards diurnal activity. In line with this prediction, all fish were predominantly nocturnal, but salmon preparing to migrate to the sea, which would experience size-dependent mortality during the forthcoming migration, were more diurnal than fish of the same age and size that were delaying migration for a further year. Moreover, the proportion of activity by day was negatively correlated with body size within the intending migrants. It has previously been shown that overwinter survival in fish delaying migration is maximized not by growth but by minimizing exposure to predators. As predicted, daytime activity in these fish was correlated with the prior rate of weight loss, fish being more diurnal when their risk of starvation was greater. To our knowledge, these are the first quantitative demonstrations of state-dependent variation in the timing of daily activity.

Keywords: Atlantic salmon; *Salmo salar*; diel activity; predation risk; foraging; growth

1. INTRODUCTION

Most animals are adapted to a consistently diurnal, nocturnal or crepuscular lifestyle, and have evolved circadian activity rhythms to match these adaptations (Thorpe 1978; Helfman 1993). Intraspecific variation in such activity patterns is generally confined to the precise timing of the active period rather than any overall shift in the diel schedule itself. However, fish are known to exhibit pronounced variation, with some individuals being predominantly nocturnal while others under the same conditions are mostly active by day, although the causes of this variation have not been known (Sánchez-Vázquez *et al*. 1995; Brännäs & Alanärä 1997; Alanärä & Brännäs 1997). Here, we show that the scheduling of daytime versus night-time activity by Atlantic salmon, *Salmo salar*, in winter varies according to the life-history strategy they have adopted and their future mortality risk; to our knowledge, this is the first demonstration of size-independent but state-dependent diel activity patterns.

Whether animals are active by day or by night should depend on the relative costs and benefits of activity at these opposing times. For prey species in the non-breeding season, this is based on diel variation in both potential feeding rate and predation risk (Clark & Levy 1988). In the case of juvenile salmon, which are visual foragers in freshwater streams, their maximum feeding rate is much greater by day than by night, owing to their impaired ability to see passing prey items at low light intensities (Fraser & Metcalfe 1997). However, in winter this is countered by an increased predation risk by day as their most important predators are diurnal (Fraser *et al*. 1993). Diurnal foraging is thus more profitable in terms of food gained per unit time, but also riskier than nocturnal foraging (Clark & Levy 1988). Because, in common with most prey species, juvenile salmon are able to take refuge from predators when not feeding (in this case by hiding in crevices in the streambed (Gardiner & Geddes 1980; Rimmer *et al*. 1983; Valdimarsson *et al*. 1997)), the extent and timing of their activity in winter should be based on the optimal trade-off between the need to avoid predation (by hiding) and the need for food (Bull *et al*. 1996). Fish, being ectotherms, have very low maintenance requirements at cold winter temperatures and so their food intake can vary widely from a sustained daily intake that maximizes their growth rate to a prolonged period of complete fasting (Weatherley & Gill 1987). Therefore, the need for food (and hence timing of daily activity) should vary between individual salmon according to both their current nutritional state and the benefits they will obtain from growth, both of which depend on the life-history strategy they adopt.

The age at which juvenile salmon metamorphose and undertake the spring seaward migration is flexible. The decision as to whether or not to migrate in a given year is made some nine months prior to the event, after which point a cohort is divided into those fish that will migrate at the next opportunity and those that will delay for at least another year ('early' and 'delayed' migrants, respectively (Thorpe 1977; Metcalfe *et al*. 1990)). The survival rate of migrants is positively correlated with body size at the time

*Author for correspondence (n.metcalfe@bio.gla.ac.uk).

Received 13 March 1998 *Accepted* 21 April 1998

of their downstream migration (Mangel 1996), owing to both size-dependent predation (Feltham 1990) and the stress of osmoregulation in seawater being dependent on the ratio of body weight to surface area (Thorpe & Metcalfe 1998). There is therefore a selection pressure against small body size in migrants, but the relative increase in survival per unit size increment is a declining function of body size (Mangel 1996). Therefore, we predict first that diurnal activity in the winter before migration should be negatively correlated with body size, because the smaller a fish's current body size, the more it would gain from growth in the months leading up to migration.

However, the survival rate of those fish that will remain in the river for at least a further year (i.e. delayed migrants) is maximized if they merely eat enough over the winter to prevent starvation (Bull *et al*. 1996), as they readily compensate for any shortfall in growth over the winter by feeding intensively during the spring and summer when environmental conditions are much better for growth (Simpson *et al*. 1997). Delayed migrants thus enter a state of natural anorexia in autumn (Metcalfe *et al*. 1986; Metcalfe & Thorpe 1992) such that their food intake is insufficient to maintain body weight over the winter (Bull *et al*. 1996). This weight loss is regulated so that the appetite of the fish is proportional to the deficit in their nutritional reserves relative to those expected for that time of the winter (Metcalfe & Thorpe 1992; Bull *et al*. 1996). Our second prediction was that delayed migrants should therefore be more nocturnal than early migrants, as their need for food is less and so they can exploit the safer if less productive foraging time. The third prediction was that the extent of diurnal activity in delayed migrants should correlate not with current body size but with the risk of death through subsequent starvation (i.e. be negatively correlated with current nutritional state). Here, we report on experimental tests of these novel predictions.

2. METHODS

The experiments used underyearling sibling salmon that were the offspring of wild adults caught in the Loch Lomond catchment, west Scotland. The experimental fish were raised under ambient light and temperature conditions in tanks at the University Field Station, Rowardennan, and were categorized on 3 October 1995 into the two different life-history strategies on the basis of their position in a bimodal size frequency distribution (Thorpe 1977). This age-independent size separation of early and late migrants allows a very reliable categorization of the fish in the autumn prior to the spring migration of the early migrants (Thorpe 1977; Metcalfe *et al*. 1989; Heggenes & Metcalfe 1991; Nicieza *et al*. 1991). However, this also introduced body size (i.e. weight) as a potential confounding factor in the comparison of activity patterns of early and late migrants, as early migrants are larger than late at this time. Therefore, to remove this effect, the weights of the two categories of tested fish were made similar after they had been categorized and before they were tested for winter activity patterns by maintaining early migrants at 5.3 ± 0.03 °C from 3 to 31 October, whereas delayed migrants remained at ambient temperatures (13.3 °C declining to 11.5 °C; mean $= 12.6 \pm 0.1$ °C). All fish were given access to food *ad libitum* throughout, but the temperature difference alone achieved the desired manipulation in growth rates so that the size disparity between the two categories of fish was removed by the end of October (early migrants $= 5.99 \pm 0.35$ g ($n = 17$), late migrants $= 5.44 \pm 0.32$ g ($n = 14$), $t = 1.15$, $p = 0.26$).

In winter, juvenile salmonids hide in streambed refuges when not foraging (Fraser *et al*. 1993; Heggenes *et al*. 1993). Activity patterns were therefore measured in a testing tank with a distinct darkened refuge (a lightproof plastic container, 10 cm diameter by 15 cm deep) positioned directly below one corner of a lit and open foraging area (1 m square, water depth 30 cm), to which it was linked by a narrow vertical tube (3.5 cm internal diameter, 30 cm long). A small amount of food, in the form of commercial salmon pellets (Fulmar feed, BOCM Pauls Ltd), automatically trickled into the foraging area every 10 min throughout the day and night. Uneaten food was washed down a central drain by the current. Water velocities within the foraging habitat were less than 10 cm s^{-1}, and so were within the preferred range for juvenile salmon at night-time light intensities (Metcalfe *et al*. 1997). Fish therefore had the same situation of choosing between an exposed foraging habitat, the open tank, or a 'streambed' refuge that contained no food. Previous studies have shown that fish from wild parents that are reared in the laboratory retain pronounced antipredator responses (Metcalfe *et al*. 1987; Magurran 1990). These include avoidance where possible of potentially dangerous habitats even in the absence of predators, as animals have evolved inherent behaviour patterns that take account of anticipated (rather than observed) predation risks, and when given imperfect knowledge should always tend towards overestimating predation hazard, as this is less risky than the reverse (Bouskila & Blumstein 1992). Therefore, we were confident that the fish would attempt to minimize the time spent in the exposed foraging area.

Individual activity patterns were monitored automatically by using passive integrated transponder (PIT) tags that were uniquely coded. A PIT tag was implanted into the abdominal cavity of each fish, so that the timing and direction of each movement between the refuge and foraging area could be detected by two PIT antennae wrapped around the vertical tube. The antennae were interrogated alternately every 200 ms by an automated system that logged the identity of any tagged fish passing the antennae onto computer (Burns *et al*. 1997). The antennae were very reliable, logging a minimum of 97.0% of all outgoing movements from the refuge and 98.4% of return movements (Burns *et al*. 1997). Opaque screens around the testing area prevented any disturbance to the fish. All fish were kept at the test temperature (5.4 ± 0.1 °C) and photoperiod (12L:12D; light levels 450 lx and 0.1 lx, respectively) for a minimum of three weeks before monitoring activity, so that they acclimatized to the conditions. This period is longer than the minimum considered necessary for temperature acclimation in juvenile salmon (Elliott 1981). Activity was then recorded for five complete days; early migrants were tested separately from delayed migrants to prevent competition affecting the activity rhythms of the fish. To obtain information on body size, all fish were weighed to the nearest 0.01 g immediately before the five-day period of data recording; delayed migrants were also weighed four weeks before this to determine their recent rate of weight loss as a proxy for physiological state (see Gardiner & Geddes 1980; Weatherley & Gill 1987).

3. RESULTS

As expected, the fish showed a preference for using the refuge rather than the exposed foraging habitat: on

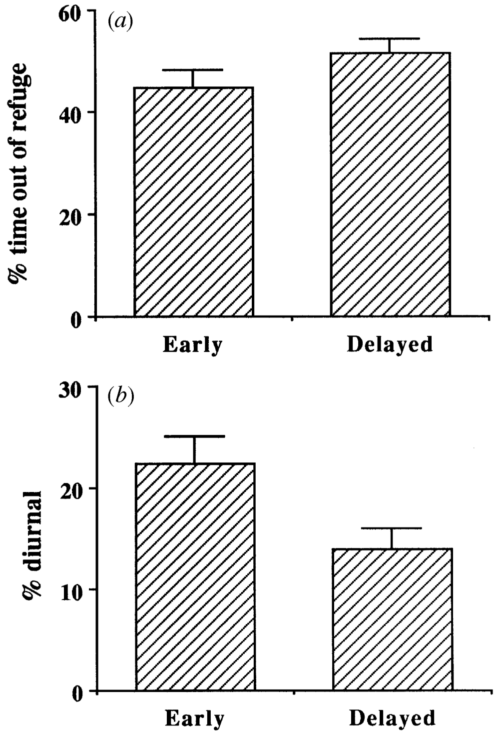

Figure 1. Winter diel activity patterns of Atlantic salmon in relation to life history adopted. (*a*) There was no difference in the overall percentage of time spent out of the refuge per 24 h by early migrants ($n=17$) and delayed migrants ($n=14$) of the same mean size and age. (*b*) However, early migrants were more diurnal than were delayed migrants (% diurnal is per cent of time outside refuge that was during daylight). Data presented as means+s.e.; see text for statistical analysis.

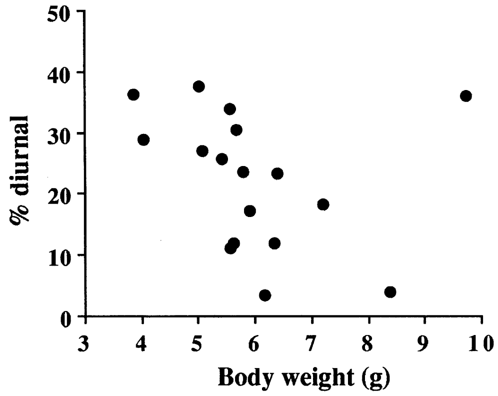

Figure 2. The relationship between diel timing of activity and current body size in early migrant salmon. Small fish were more likely to be active during the daytime (% diurnal is per cent of time outside refuge that was during daylight; see text for statistical analysis).

average, they spent 59.3% ($n=31$ fish) of their time in the refuge, despite it being less than 0.5% of the volume of the foraging area. Interestingly, there was no difference between early and delayed migrants in the total percentage of time (day and night combined) that they spent out of the refuge (figure 1*a*; Mann–Whitney *U*-test, $U=91.0$, $p=0.27$). However, the time of day at which the two categories of fish were active differed as predicted: when daytime activity (i.e. time out of the refuge) of each individual fish was expressed as a percentage of all of its activity, early migrants were found to be significantly more diurnal in their behaviour (figure 1*b*; Mann–Whitney *U*-test, $n=17$ early and 14 delayed migrants, $U=65.0$, $p=0.03$).

A further prediction was also upheld, in that the degree to which fish were day-active was negatively correlated with their current body weight in early migrants (figure 2; Spearman rank correlation, $r_s=-0.492$, $n=17$, $p<0.05$) but not in delayed migrants ($r_s=0.182$, $n=14$, $p=0.53$). All fish were given free access to food throughout the entire experiment, but whereas early migrants continued to grow, the majority of delayed migrants lost weight. In these fish the diel schedule of activity was, as predicted, related to the rate of early winter weight loss (expressed as the percentage change in weight per day over the preceding four weeks). Those delayed migrants that had lost the greatest percentage of their previous body weight did not increase their general level of foraging activity (correlation between the percentage change in weight and total percentage of time spent out of the refuge: $r_s=-0.350$, $n=14$, $p=0.22$), but instead shifted the timing of activity so that they were more active in the day (figure 3; $r_s=-0.675$, $n=14$, $p=0.008$).

4. DISCUSSION

All fish used the darkened refuge extensively, despite the fact that it was small and contained no food. They thus used it as a place of concealment (Valdimarsson & Metcalfe 1998) in a manner analogous to the substratum refuges used in the wild. Salmon rely on vision to detect their prey, and under the night-time light intensities prevailing in this experiment (0.1 lx, equivalent to moonlight (Fraser & Metcalfe 1997)) they would only be able to feed at *ca.* 35% of their daytime efficiency (Fraser & Metcalfe 1997). Despite this, there was an overall preference for being active by night, presumably because the perceived predation risk was far greater by day (Clark & Levy 1988; Fraser *et al.* 1993). However, there was significant variation between individual fish, not in the total amount of activity per day, but in the proportion of that activity that was nocturnal, and this corresponded predictably with their current physiological state and life-history pattern: fish that were preparing to migrate tended more towards diurnal activity especially if relatively small, whereas delayed migrants were more diurnal if they were in a poorer physiological condition.

These individual differences in response to a given habitat are a consequence of the fact that the trade-off between foraging and predator avoidance is not fixed but varies according to an individual's physiological state and life-history strategy. Therefore, while foraging by night may offer the lowest ratio of mortality risk to food gained (see Gilliam & Fraser 1987; Clark & Levy 1988), this is not necessarily the optimal time-period of feeding for all fish, as the strategy that will maximize their long-term survival varies. Thus, some must achieve a higher intake than is possible from purely nocturnal foraging, and so must forage more by day even though that is riskier in the short-term.

There is circumstantial evidence that these state-dependent foraging decisions are a real phenomenon in

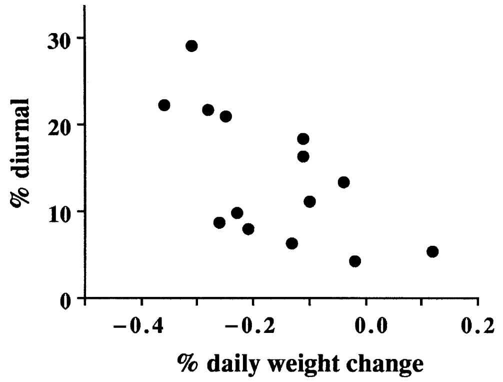

Figure 3. The relationship between diel timing of activity and percentage daily weight change of delayed migrant salmon over the previous four weeks. Diurnal activity was greatest in individuals that had lost most weight (see text for statistical analysis).

wild fish. Nicieza & Braña (1993) found that the extent of late winter growth in salmon preparing to migrate was strongly and negatively correlated with their body size at the onset of winter, with small intending migrants growing fast in the months leading up to migration, whereas the largest fish did not grow at all. This suggests that growth rates of individuals in natural populations may be maintained not at their maximal level, but at a level which takes account of the costs and benefits of achieving a given growth rate (which will vary between individuals). The ability of smaller fish to mitigate their size disadvantage by disproportionately increasing their growth rate by exhibiting compensatory growth only comes at the cost of an increased exposure to predators (Nicieza & Metcalfe 1997): small fish must take increased risks in the short-term if they are to avoid the greater costs of small body size in the long-term. Such size-dependent risk taking in relation to diel activity schedules has been noted in the field by Gries *et al.* (1997), who found that underyearling (i.e. smaller) wild, juvenile, salmon were far less likely to be hiding in refuges during the day than were yearlings in the same stream. Activity patterns can thus be considerably more complex and flexible than might be assumed from an assessment of a species' typical mode of foraging.

We thank the Loch Lomond Angling Improvement Association for provision of fish eggs, V. Cameron, R. MacDonald and J. Laurie for help with fish husbandry, and BOCM Pauls for providing fish food. This study was funded by a grant from the Natural Environment Research Council to N.B.M.

REFERENCES

Alanärä, A. & Brännäs, E. 1997 Diurnal and nocturnal feeding activity in arctic char and rainbow trout. *Can. J. Fish. Aquat. Sci.* **54**, 2894–2900.

Bouskila, A. & Blumstein, D. T. 1992 Rules of thumb for predation hazard assessment—predictions from a dynamic model. *Am. Nat.* **139**, 161–176.

Brännäs, E. & Alanärä, A. 1997 Is diel dualism in feeding activity influenced by competition between individuals? *Can. J. Zool.* **75**, 661–669.

Bull, C. D., Metcalfe, N. B. & Mangel, M. 1996 Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. *Proc. R. Soc. Lond.* B **263**, 13–18.

Burns, M. D., Fraser, N. H. C. & Metcalfe, N. B. 1997 An automated system for monitoring fish activity patterns. *Trans. Am. Fish. Soc.* **126**, 1036–1040.

Clark, C. W. & Levy, D. A. 1988 Diel vertical migrations by juvenile sockeye salmon and the anti-predation window. *Am. Nat.* **131**, 271–290.

Elliott, J. M. 1981 Some aspects of thermal stress on freshwater teleosts. In *Stress and fish* (ed. A. D. Pickering), pp. 209–245. London: Academic Press.

Feltham, M. J. 1990 The diet of red-breasted mergansers, *Mergus serrator*, during the smolt run in N.E. Scotland: the importance of salmon *Salmo salar* smolts and parr. *J. Zool.* **219**, 113–122.

Fraser, N. H. C. & Metcalfe, N. B. 1997 The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Funct. Ecol.* **11**, 385–391.

Fraser, N. H. C., Metcalfe, N. B. & Thorpe, J. E. 1993 Temperature-dependent switch between diurnal and nocturnal foraging in salmon. *Proc. R. Soc. Lond.* B **252**, 135–139.

Gardiner, W. R. & Geddes, P. 1980 The influence of body composition on the survival of juvenile salmon. *Hydrobiologia* **69**, 67–72.

Gilliam, J. F. & Fraser, D. F. 1987 Habitat selection under predation hazard—test of a model with foraging minnows. *Ecology* **68**, 1856–1862.

Gries, G., Whalen, K. G., Juanes, F. & Parrish, D. L. 1997 Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning. *Can. J. Fish. Aquat. Sci.* **54**, 1408–1413.

Heggenes, J. & Metcalfe, N. B. 1991 Bimodal size distributions in wild juvenile Atlantic salmon populations and their relationship with age at smolt migration. *J. Fish Biol.* **39**, 905–907.

Heggenes, J., Krog, O. M. W., Lindås, O. R., Dokk, J. G. & Bremnes, T. 1993 Homeostatic behavioural responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. *J. Anim. Ecol.* **62**, 295–308.

Helfman, G. S. 1993 Fish behaviour by day, night and twilight. In *Behaviour of teleost fishes* (ed. T. J. Pitcher), pp. 479–512. London: Chapman & Hall.

Magurran, A. E. 1990 The inheritance and development of minnow anti-predator behaviour. *Anim. Behav.* **39**, 834–842.

Mangel, M. 1996 Computing expected reproductive success of female Atlantic salmon as a function of smolt size. *J. Fish Biol.* **49**, 877–882.

Metcalfe, N. B. & Thorpe, J. E. 1992 Anorexia and defended energy levels in over-wintering juvenile salmon. *J. Anim. Ecol.* **61**, 175–181.

Metcalfe, N. B., Huntingford, F. A. & Thorpe, J. E. 1986 Seasonal changes in feeding motivation of juvenile Atlantic salmon (*Salmo salar*). *Can. J. Zool.* **64**, 2439–2446.

Metcalfe, N. B., Huntingford, F. A. & Thorpe, J. E. 1987 The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Anim. Behav.* **35**, 901–911.

Metcalfe, N. B., Huntingford, F. A., Graham, W. D. & Thorpe, J. E. 1989 Early social status and the development of life-history strategies in Atlantic salmon. *Proc. R. Soc. Lond.* B **236**, 7–19.

Metcalfe, N. B., Huntingford, F. A., Thorpe, J. E. & Adams, C. E. 1990 The effects of social status on life-history variation in juvenile salmon. *Can. J. Zool.* **68**, 2630–2636.

Metcalfe, N. B., Valdimarsson, S. K. & Fraser, N. H. C. 1997 Habitat profitability and choice in a sit-and-wait predator: juvenile salmon prefer slower currents on darker nights. *J. Anim. Ecol.* **66**, 866–875.

Nicieza, A. G. & Braña, F. 1993 Compensatory growth and optimum size in one-year-old smolts of Atlantic salmon (*Salmo salar*). In *Production of juvenile salmon, Salmo salar, in natural waters*, vol. 118 (ed. R. J. Gibson & R. E. Cutting), pp. 225–237.

Nicieza, A. G. & Metcalfe, N. B. 1997 Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. *Ecology* **78**, 2385–2400.

Nicieza, A. G., Braña, F. & Toledo, M. M. 1991 Development of length-bimodality and smolting in wild stocks of Atlantic salmon, *Salmo salar* L., under different growth conditions. *J. Fish Biol.* **38**, 509–523.

Rimmer, D. M., Paim, U. & Saunders, R. L. 1983 Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. *Can. J. Fish. Aquat. Sci.* **40**, 671–680.

Sánchez-Vázquez, F. J., Madrid, J. A. & Zamora, S. 1995 Circadian rhythms of feeding activity in sea bass, *Dicentrarchus labrax* L.: dual phasing capacity of diel demand-feeding pattern. *J. Biol. Rhythms* **10**, 256–266.

Simpson, A. L., Metcalfe, N. B., Huntingford, F. A. & Thorpe, J. E. 1997 Pronounced seasonal differences in appetite of Atlantic salmon parr, *Salmo salar*: effects of nutritional state and life-history strategy. *Funct. Ecol.* **10**, 760–767.

Thorpe, J. E. 1977 Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *J. Fish Biol.* **11**, 175–184.

Thorpe, J. E. 1978 *Rhythmic activity in fishes*. London: Academic Press.

Thorpe, J. E. & Metcalfe, N. B. 1998 Is smolting a positive or a negative developmental decision? *Aquaculture*. (In the press.)

Valdimarsson, S. K. & Metcalfe, N. B. 1998 Shelter selection in juvenile Atlantic salmon; or why do salmon seek shelter in winter? *J. Fish Biol.* **52**, 42–49.

Valdimarsson, S. K., Metcalfe, N. B., Thorpe, J. E. & Huntingford, F. A. 1997 Seasonal changes in sheltering: effect of light and temperature on diel activity in juvenile salmon. *Anim. Behav.* **54**, 1405–1412.

Weatherley, A. H. & Gill, H. S. 1987 *The biology of fish growth*. London: Academic Press.